Hierarchical ordering of reticular networks

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Abstract

The structure of hierarchical networks in biological and physical systems has long been characterized using the Horton-Strahler ordering scheme. The scheme assigns an integer order to each edge in the network based on the topology of branching such that the order increases from distal parts of the network (e.g., mountain streams or capillaries) to the "root" of the network (e.g., the river outlet or the aorta). However, Horton-Strahler ordering cannot be applied to networks with loops because they they create a contradiction in the edge ordering in terms of which edge precedes another in the hierarchy. Here, we present a generalization of the Horton-Strahler order to weighted planar reticular networks, where weights are assumed to correlate with the importance of network edges, e.g., weights estimated from edge widths may correlate to flow capacity. Our method assigns hierarchical levels not only to edges of the network, but also to its loops, and classifies the edges into reticular edges, which are responsible for loop formation, and tree edges. In addition, we perform a detailed and rigorous theoretical analysis of the sensitivity of the hierarchical levels to weight perturbations. We discuss applications of this generalized Horton-Strahler ordering to the study of leaf venation and other biological networks.

Keywords. complex networks, spatial networks, graph theory, redundancy

Introduction

Networks and network theory have been utilized to represent and analyze the structure and function of a myriad of biological systems. These systems span scales from cells to ecosystems and include gene regulatory networks [6, 4], metabolic pathways [27, 22], disease dynamics [38, 36], food webs [41, 2], host-parasite webs [33, 24], and social interactions [57, 18, 15]. In the process, structural archetypes have been identified including scale-free behavior, motifs, modularity, the emergence of hubs, and small-world structure [57, 7, 52, 26, 1, 39, 40, 3]. However, these theories do not typically incorporate the spatial constraints that underlie the location and connections amongst nodes and edges. Indeed, there are many examples of delivery and distribution networks where nodes and edges are physical structures embedded in space, e.g., leaf venation networks [55, 11], cardiovascular networks [32, 29], cortical networks [59], root networks [56], ant trails [34] and road networks [35]. Hence, theory is also needed to characterize biological networks whose structure is strongly influenced by physical constraints (for a review, see [8]).

Although the theory of spatial networks is quite diverse, the theory as applied to resource delivery networks in biology often involves certain simplifying assumptions. For example, in fractal branching theory, a network is seen as a perfectly self-similar structure, e.g. a dividing binary tree [46]. A prominent theory of metabolic scaling in mammals assumes the cardiovascular system is a fractal whose physical dimensions have evolved to optimally transport fluid from the aorta to capillaries [58, 13]. An extension of this model to the above-ground structure of tree branches makes similar assumptions [23]. Both models have inspired a wide array of follow-up work with increased recognition that the original fractal branching assumption is overly simplistic [21, 44, 50, 5, 31]. For example, in reality, physical networks in biology have side branches and are not perfectly balanced binary trees [55]. Theories of side-branching resource delivery and distribution networks have their origins in the study of river networks. In a river network, streams merge together to form larger streams. However, small streams can merge into larger streams of all scales. The topological structure of river

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networks can be analyzed using the so-called Horton-Strahler order [28, 51]. This scheme assigns an integer number to every branch of the network. The numbers represent different levels of the branch hierarchy, with larger numbers corresponding to the larger stream segments in the network. The Horton-Strahler ordering is the basis for the characterization of the statistical properties of river networks[20], including the finding that river networks are fractal [47]. Moreover, the side-branching statistics first introduced by Tokunaga [54] can be used to characterize universal features of river networks and departures thereof [19].

Leaf venation networks are a prominent example of a physical delivery and distribution network whose structure possess numerous side branches. The structure of leaf venation networks has broad functional implications. For example, leaf vein density is positively correlated with photosynthetic rates [12] and also influences the extent to which leaves form a hydraulic bottleneck in whole plants [16, 48]. However, many leaves of higher plants (notably most leaves of angiosperm lineages), have reticulate venation networks, involving loops within loops [11]. It has been hypothesized that reticulate patterns allow leaves to maintain the supply of water and nutrients to and from photosynthetically active chloroplasts even when flow through some edges in the network is lost [37, 30, 49, 17] due to mechanical damage or herbivory. Unfortunately, the Horton-Strahler ordering scheme developed for the analysis of river networks is not directly applicable to reticular networks. The reason is that loops lead to inconsistencies in the merging procedure in which a strictly hierarchical order is assigned to all edges.

In this paper we propose a method that generalizes the Horton-Strahler order to planar, weighted reticular networks. Such networks encompass a large class of physical networks, where weights can often be obtained by estimating dimensions of edges, such as branch widths, or other indicators of cost or importance. While coinciding with the Horton-Strahler order for branching networks, our method also assigns hierarchical levels to the loops of the network. Moreover, it categorizes the branches into the ones responsible for the formation of loops, and the ones forming the tree structure of the network. Edge weights play an important role in our algorithm, and we perform a theoretical analysis of possible effects of weight perturbations on the hierarchical levels. We find that the loop hierarchy is more robust to measurement error of network edge weights than is the tree hierarchy. In the past, comparisons of the statistical similarity between river networks and leaves have been proposed, albeit such comparisons are restricted to leaves without loops [43]. Hence, we also discuss applications of the current method to the characterization and comparison of reticulate leaf venation networks as

well as obstacles to extending this method to a more general class of networks.

A graph theoretic approach to Horton-Strahler ordering of rooted trees

We start by reviewing the algorithm for constructing the Horton-Strahler order. For the remainder of the paper, we shall adopt the language of graph theory [14, 10]. Note that in graph theory, the "leaves" of the network are those vertices which only have a single edge that connects to them. In this context, the input to the Horton-Strahler ordering algorithm is simply a rooted tree, $T = (V, E)$, where V is the set of vertices and E is the set of edges. Given such a tree, the algorithm assigns a level, $\lambda(e)$, to each edge $e \in E$ in the following way:

- Assign level 1 to all edges connected to the leaves of T.

- For each vertex having only one incident edge, e, with undefined $\lambda(e)$, let l be the maximal level among the other incident edges. If there is a single incident edge of level l, then $\lambda(e) = l$. If there are two or more incident edges of level l, then $\lambda(e) = l + 1$.

The result of this algorithm is illustrated in Fig. 1(a). Conventionally in the study of river networks [47], this algorithm can be summarized by a single rule which states that the order of a downstream segment is equal to

$$\lambda = \max(\lambda_1, \lambda_2) + \delta_{\lambda_1, \lambda_2}$$

where λ_1 and λ_2 are the order of the two upstream segments that are merging and δ is the Kronecker delta.

It is clear, however, that if the network has loops, as in Fig. 1(b), the algorithm simply cannot proceed because there always will be a vertex having more than one incident edge with an undefined level. Moreover, loops in this graph seem to also form a hierarchy. For example, the loop outlined in Fig. 1(b) by the red dotted line may belong to a higher level than the loop outlined by the blue dashed line. It turns out that such a hierarchy can be constructed and separated from the tree hierarchy if edges have weights and the graph itself is planar. An example of such a graph is shown in Fig. 1(c), where the weights represent widths of the branches.

To guide the reader's intuition, we first provide an alternative description of the Horton-Strahler algorithm for the case when the tree T is binary and weighted. Let $w : E \rightarrow \mathbb{R}$ be the weight function, that is, $w(e)$ is the weight of an edge $e \in E$. Since the tree is rooted, there is a partial order defined on E as follows: $e_1 \leq e_2$ if there
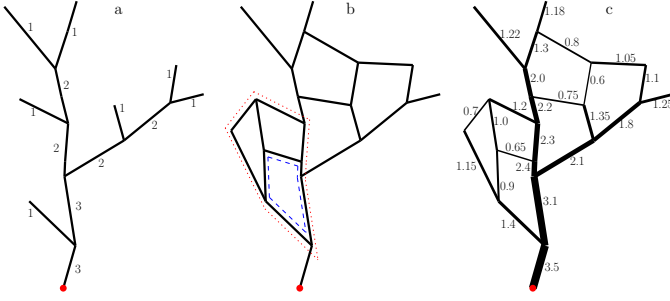
Figure 1: Examples of networks with hierarchical structure with a common "root" or outlet denoted by the red dot at the bottom of each network: (a) Horton-Strahler stream order of branch hierarchy in a tree network; (b) Reticular network with possible loop hierarchy: the, blue, dashed loop might be less important than the red, dotted loop; (c) Reticular network of (b) with weights.

is a path from the root to e_1 which passes through e_2 (in other words, e_2 is closer to the root than e_1). Let us assume that the weight function is strictly increasing with respect to this order, that is, $w(e_1) < w(e_2)$ if $e_1 < e_2$. In this case, the Horton-Strahler order can be computed using the following procedure:

- Let $C \subset E$ be the set of edges incident to leaves of T, regarded as a set of disjoint components. For each $e \in C$ let $\lambda(e) = 1$.

- Iterate through (the rest of the) edges in order of increasing weight. For each edge e do the following:

  - If e shares a vertex with a single component $c_1 \in C$, then merge c_1 and e into a new component c, and let $\lambda(e) = \lambda(c) = \lambda(c_1)$.

  - If e shares a vertex with two components $c_1, c_2 \in C$, then merge c_1, c_2, and e into a new component c, and assign levels as follows:

    * If $\lambda(c_1) = \lambda(c_2)$, then $\lambda(c) = \lambda(c_1) + 1$.
    * If $\lambda(c_1) \neq \lambda(c_2)$, then $\lambda(c) = \max\{\lambda(c_1), \lambda(c_2)\}$.
    * $\lambda(e) = \lambda(c)$.

Ordering of planar weighted graphs

We now present the algorithm for constructing the generalized Horton-Strahler order. Let $G = (V, E)$ be a planar graph, not necessarily a tree, and again let $w : E \to \mathbb{R}$ be a weight function. We shall assume that w is injective (i.e., all weights are unique). Otherwise, the ties will be resolved arbitrarily. The merging procedure for computing the Horton-Strahler order works with disjoint components, which, in the language of algebraic topology, are 0-dimensional homology classes.
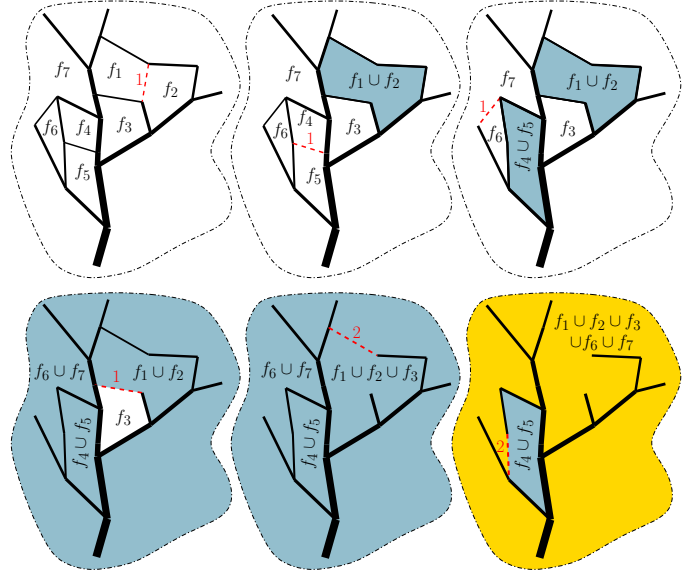

Figure 2: An illustration of the loop merging procedure applied to the graph from Fig. 1(c). Red, dashed edges are the ones removed during merging, the corresponding numbers show their levels. Levels of faces is encoded by the color: white faces have level 1, light blue faces have level 2, and gold faces have level 3. Note that f_7 is the unbounded face.

Loops, on the other hand, are 1-dimensional homology classes. Hence, we may try to construct a hierarchy by merging loops. Notice that the boundary of a face of the graph G is a loop, and we can merge two neighboring faces by removing a shared edge. Using these two observations, we obtain the following merging procedure for loops:

- Sort the edges so that $w(e_1) < w(e_2) < \cdots < w(e_n)$, where $n = |E|$ is the number of edges.

- Let $\lambda(f) = 1$ for each face f.

- Iterate through $e_1, \ldots, e_n$ and do the following:

  - If e_i is adjacent to a single face, skip to the next edge.

  - If e_i is adjacent to two distinct faces f_L and f_R, remove e_i from the graph, let $f_{merged} = f_L \cup f_R$, and assign the levels as follows:

    * If $\lambda(f_L) = \lambda(f_R)$ then $\lambda(f_{merged}) = \lambda(f_L) + 1$.
    * If $\lambda(f_L) \neq \lambda(f_R)$ then $\lambda(f_{merged}) = \max\{\lambda(f_L), \lambda(f_R)\}$.
    * $\lambda(e_i) = \min\{\lambda(f_L), \lambda(f_R)\}$.

A step-by-step illustration of loop merging applied to the tree in Fig. 1(c) is shown in Fig. 2. Notice that this procedure builds a rooted binary tree, where leaves correspond to the faces of G, and the rest of the vertices

correspond to unions of these faces. The assignment of levels in this tree follows the original Horton-Strahler algorithm. It is also useful to remember that faces of G are vertices of its dual graph, G^*, and merging faces of G can be thought of as adding an edge to G^*. Hence, the two merging procedures that we described are, in some sense, dual. We shall refer to the binary tree of faces as the *co-tree* of G, and denote it by $T^*(G)$.

The construction of $T^*(G)$ removes edges from G which are responsible for the existence of loops. We shall call such edges *reticular*. Assignment of levels for such edges is based on the assumption that a merger should not be more significant than any of the merging elements. Notice that after removing reticular edges from G we have a spanning tree of G, which we denote by $T(G)$. This tree captures the tree-like structure of the original network, and we can assign hierarchical levels to its edges using the original Horton-Strahler algorithm. We only need to determine which vertex should be the root, and we do this by finding the vertex with a single incident weight of maximum weight. Hence, we augment the procedure for constructing the loop hierarchy by the following statement:

- Apply the Horton-Strahler ordering to the remainder of the graph (which is a rooted tree).

The result of the complete algorithm applied to the tree in Fig. 1(c) is provided in Fig. 3.

The algorithm produces three types of output. First, it provides a unique set of orders to those edges involved in the non-reticulate component of the network (Figure 3 - left panel). Second, it provides a unique set of orders to those edges involved in the formation of loops (Figure 3 - right panel). Further, one can also calculate the side-branching statistics associated with both orderings. The side-branching statistics, i.e., "Tokunaga" statistics [54], for a conventional non-loopy tree are summarized by the numbers N_{ij} which are the number of edges of level j that join with edges of level i. Because of the ordering process, these statistics are evaluated for $i > j$. These numbers can also be divided by the number of absorbing edges, i.e., the total number of edges of level i to yield an average number of side-branches per segment. Here, the algorithm produces two sets of Tokunaga statistics, the numbers N_{ij} for the side-branching of tree edges (Figure 3 - left panel) and M_{ij} for the side-branching of reticulate edges (Figure 3 - right panel).

Sensitivity of planar network ordering to weight perturbations

Clearly, edge weights play an important role in the construction of both loop and tree hierarchies. Unfortu-
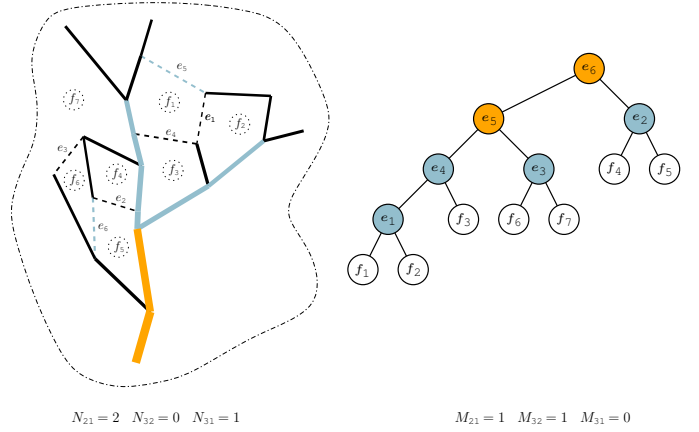

Figure 3: Hierarchical levels assigned to the loops and branches of the network from Fig. 1(c). Edge levels are shown on the left, where black edges have order 1, light blue edges have order 2 and gold edges have order 3; reticular edges are dashed. Face levels are shown in the co-tree on the right, where white nodes have order 1, light blue nodes have order 2 and gold nodes have order 3. Leaves of the co-tree are labeled by the corresponding faces while other nodes are labeled by the reticular edges causing the merger of the two child nodes. Numbers N_{ij} are Tokunaga statistics for the spanning tree and indicate the number of edges of level j joining with edges of level i [54]. Similarly, M_{ij} are Tokunaga statistics for the reticulate co-tree and indicate the number of edges and faces of level j merging with edges of level i. For both M and N, statistics are only collected when $i > j$.

nately, weight estimation done in practice is often imprecise, so the order in which the algorithm iterates through the edges may be perturbed. In this section we investigate how such a perturbation affects the loop and tree hierarchies.

We start by considering the worst possible change in the hierarchical levels of loops. Notice that the highest level in the hierarchy of loops can be as low as 2. This happens when the first reticular edge creates a level 2 face and every other reticular edge merges a level 1 face with the only level 2 face (see Fig. 4(a)). On the other hand, the highest level in the loop hierarchy can be as high as $\log(m)$, where m is the number of faces. This happens when level 1 faces are merged only with level 1 faces until only faces of level 2 are left, then level 2 faces are merged with level 2 faces until only faces of level 3 are left, and so on (see Fig. 4(b)). It is clear from the example in Fig. 4 that there is a permutation of edges that can change the loop hierarchy from one of the extreme cases to the other. However, in practice such a permutation would generally result in from a significant perturbation in weights. For small perturbations, it is more likely that only a few transpositions of edges will occur.

Let $e_1, \ldots, e_n$ be the order of edges with respect to their weights. We shall now analyze how the structure of $T(G)$ and $T^*(G)$ changes when a single transposi-
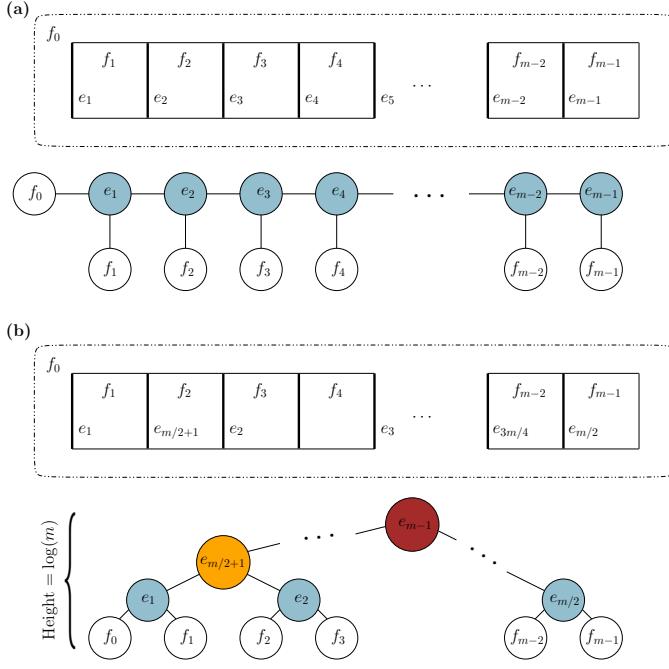
Figure 4: Example of the two extreme cases of the loop hierarchy. The network has m faces, where $m = 2^k$ for some integer $k > 0$. $(m - 1)$ of these faces are adjacent squares and the other one is the unbounded face. Vertical edges are removed before horizontal edges as follows: (a) The edges are removed sequentially from left to right. The corresponding co-tree has the shape of a "comb" and the maximal hierarchical level is 2; (b) The edges are removed from left to right skipping every second edge. The process is repeated until all vertical edges except the rightmost one are removed. The corresponding co-tree has the height $log(m) = k$ which is the maximal hierarchical level.

tion occurs, that is, when the order of e_i and e_{i+1} is swapped. First, we notice that there will be no changes to the structure of the co-tree or the spanning tree if e_i and e_{i+1} are both tree edges, or if e_i is a tree edge and e_{i+1} is a reticular edge. Hence, there are two cases to consider: when both e_i and e_{i+1} are reticular, and when e_i is a reticular edge and e_{i+1} is a tree edge. In the former case, we can regard reticular edges as edges of the co-tree. We see then that swapping the two edges may shift a subtree of the co-tree only one level up or down. Therefore, it is reasonable to expect that hierarchical levels of loops will change at most by one. The case of a reticular edge and a tree edge is more complicated. Such a transposition may lead to detaching a subtree of the remaining spanning tree and attaching it at a different place. This may have a drastic effect on the tree hierarchy. A detailed analysis of the two cases justifying the above conclusions is present below.

Case 1. e_i and e_{i+1} are both reticular. Only the co-tree can be affected in this case. Let f_i^R, f_i^L and f_{i+1}^R, f_{i+1}^L be the faces merged by removing e_i and e_{i+1}, re-

spectively. Also, let $f_i = f_i^L \cup f_i^R$ and $f_{i+1} = f_{i+1}^L \cup f_{i+1}^R$. Notice that if $f_i \neq f_{i+1}^L$ and $f_i \neq f_{i+1}^R$, then f_i is not a child of f_{i+1} in $T^*(G)$), and there will be no changes to the structure of the co-tree. Suppose that $f_i = f_{i+1}^L$ (the case when $f_i = f_{i+1}^R$ follows the same argument). Then e_{i+1} is adjacent to either f_i^L or f_i^R; let us assume it's f_i^R. Removing e_{i+1} before e_i leads to merging f_{i+1}^R with f_i^R first, and then merging the resulting face with f_i^L. The corresponding change in the tree structure, shown in Fig 5, is a single rotation around f_{i+1}. Possible changes in the levels of the nodes involved in the rotation are also shown in Fig. 5. We can see that these levels can change at most by one. However, in the worst case the change in levels may propagate up $T^*(G)$ all the way to the root.

Case 2. e_i is a reticular edge and e_{i+1} is a tree edge. Let f_i^L and f_i^R be the two faces merged by removing e_i. Notice that there will be no changes in the structure of $T(G)$ or $T^*(G)$ if e_{i+1} is not adjacent to both f_i^L and f_i^R. So, let e_{i+1} be adjacent to f_i^L and f_i^R. Then removing e_{i+1} before e_i merges the same f_i^L and f_i^R, so no changes to the structure of the co-tree happen. However, e_{i+1} turns into a reticular edges, and e_i becomes a tree edge. Consequently, the structure of the spanning tree changes. Let $E^{L,R}$ be the set of edges incident to both f_i^L and f_i^R, and let $T^{L,R}$ be the tree formed by the edges in $E^{L,R}$ and the edges connected to $E^{L,R}$ and having only f_i^L or f_i^R as an adjacent face (see Fig. 6). Removing e_{i+1} and e_i splits $T^{L,R}$ into three trees, T^L, T^R, and T^M, such that T^L and T^R are connected to the boundary of $f_i^L \cup f_i^R$, and T^M is not (Fig. 6). If e_i is removed before e_{i+1}, then T^M is connected to T^R by e_{i+1}. However, if the transposition happens and e_{i+1} is removed before e_i, then T^M is connected to T^L by e_i (Fig. 6). To understand the effect of such a change on hierarchical levels, we first assume that T^M does not contain the root of $T(G)$. Let v^R be the vertex incident to e_{i+1} and T^R, and let v^L be the vertex incident to e_i and T^L. Also, let $\lambda_{i+1} = \lambda(e_{i+1})$, where e_{i+1} is regarded as an edge in $T^M \cup e_{i+1}$ rooted at v^R, and let $\lambda_i = \lambda(e_i)$, where e_i is regarded as an edge in $T^M \cup e_i$ rooted at v^L. Denote by e^R the edge of $T(G)$ which is next to e_{i+1} in the path from e_{i+1} to the root of $T(G)$, and by e^L the edge of $T(G)$ which is next to e_i in the path from e_i to the root of $T(G)$. Then we can see that removing e_{i+1} before e_i can decrease the level of e^R by at most $\max\{1, \lambda_{i+1} - 1\}$. At the same time, the level of e^L can increase by at most $\max\{1, \lambda_i - 1\}$. In the worst case, these changes can propagate up $T(G)$ all the way to the root. The case when the root of $T(G)$ belongs to T^M can lead to more drastic changes. In this case, removing e_{i+1} before e_i leads to recomputing levels of all edges in $T(G) - T^M$ by changing the root from v^R to v^L. Again, this change can then propagate further
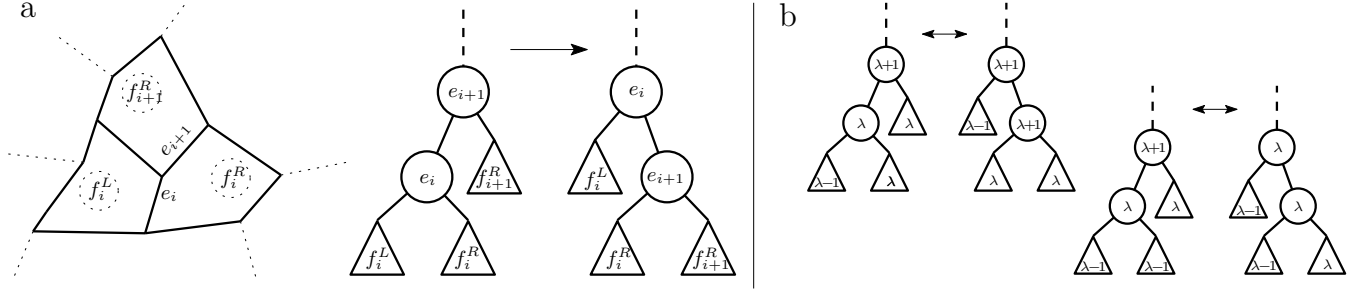
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Figure 5: Example of the effect of a single transposition of two reticular edges: (a) the part of the network containing the two edges being transposed and the effect of the transposition on the structure of the co-tree; (b) possible level changes caused by the transposition.
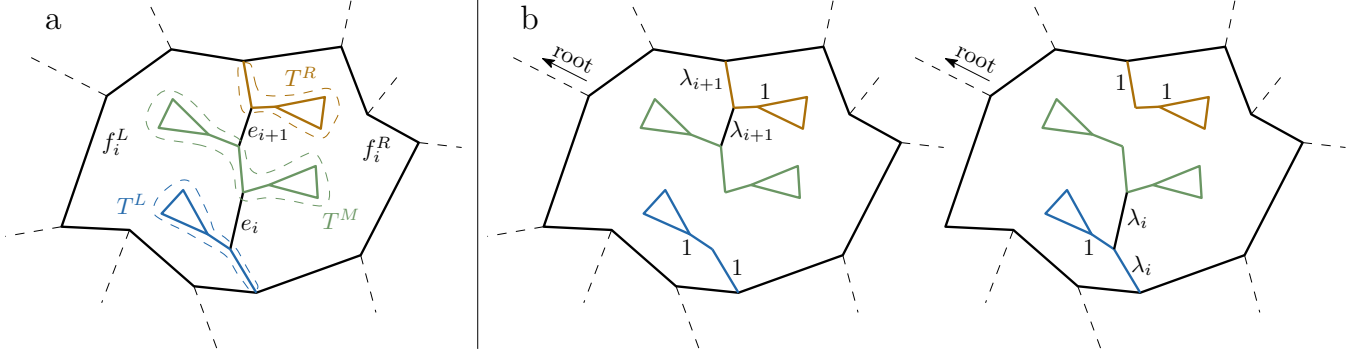

Figure 6: Example of the effect of a single transposition of a reticular edge and a tree edge: (a) The part of the network containing the two edges being transposed. The brown, blue, and green triangles (and edges) denote the subtrees adjacent to the edges. (b) The effect of the transposition on the structure of the spanning tree and its hierarchical levels.

to the root of $T(G)$.

Discussion

We have shown that the hierarchy of loops often observed in reticular physical networks can be defined explicitly using a generalization of the Horton-Strahler order. To obtain such a generalization we regard the network as a weighted graph, with weights corresponding to the widths of the network branches. Noticing that the Horton-Strahler order can be computed by analyzing how specific disjoint components (sub-networks) of a (non-reticular) network are merged as the edges are *added* in the order of increasing weight, we show that the hierarchical order of loops in a weighted planar graph can then be computed by analyzing how the *faces* of the graph are merged as we *remove* the edges in the order of increasing weight. This approach naturally classifies graph edges into reticular edges, which are responsible for loop formation, and tree edges, which constitute a spanning tree of the graph. Hence, both the loop and the tree hierarchies can be computed.

Being able to compute hierarchical levels for loops creates new possibilities for analyzing the structure of reticular networks. By means of analogy, river networks can be compared by representing their connectivity in terms of side-branching statistics [54]. These statistics depict the ways in which smaller streams connect to larger streams at all scales of the network [19]. A similar procedure could be applied to leaf networks. For example, the current algorithm decomposes reticulate networks into a binary-tree for the loop hierarchy and a separate binary tree for the tree hierarchy. Both networks have associated Horton-Strahler orders and therefore their structure can be estimated using Tokunaga statistics. Recent innovations in software now permit semi-automated extraction of the dimension and connectivity of entire leaf vein networks and the areoles that veins surround [45]. Hence, greater quantification of leaf vein networks from across a wide range of biological diversity will soon be available for which to analyze leaf development, variation across environmental gradients and in paleobotanical studies. Current attempts to compare reticulate structure have largely focused on the density of areoles (i.e., network faces) as a proxy for the "loopiness" of the network [9]. The current study will provide additional metrics to compare the detailed branching structure of reticulate networks.

An important caveat to keep in mind when comparing reticulate network structure is that estimating weights

in physical networks is by no means a trivial problem. Therefore, we have performed a theoretical analysis of possible changes in the loop and tree hierarchies due to perturbations in edge weights. We have shown that the worst possible change in the loop hierarchy is attainable, but requires a significant perturbation of weights. Taking into account that small perturbations are likely to cause only a few transpositions in the order in which the edges are removed, we have shown that a single such transposition can change the hierarchical levels of loops at most by one. We have also shown that the change in the hierarchical levels of the remaining spanning tree can be arbitrarily large even when a single transposition is performed. It is important to note that in either case the change does not happen for every transposition. Rather, the transposed edges have to satisfy a particular condition, which may happen rarely in practice. The latter claim is supported by the numerous successful applications of the Horton-Strahler order. While the method itself does not depend on any weights, the connectivity of the network is obtained by analyzing digital elevation map which contain noise [53, 42]. In particular, the difference between the correct and the computed connectivity may be exactly the same as the difference in the connectivity of our spanning tree caused by transposing two edges. Hence, the resulting hierarchy may be drastically different from the correct one. Nevertheless, the Horton-Strahler order has been successfully used for over five decades despite the potential instability identified here[28, 51, 53, 47, 20]. We suggest that empirical characterizations of reticulate planar networks include randomization analysis on edge weights to identify the robustness of claims regarding statistical structure of side-branching of the tree and co-tree.

Many biological and physical systems are represented by non-planar physical networks [25, 8] and computing hierarchical levels of loops in such networks is still an open question. While our method can be applied to obtain the tree hierarchy of such networks, the loop hierarchy cannot be computed in this case because the algorithm relies on the fact that any loop in a planar network corresponds to a union of faces. In the mathematical language, (boundaries of) faces of a planar graph form a canonical basis for loops (1-dimensional homology classes). Such a canonical basis is not present in non-planar graphs. It is not clear at this point how to handle the non-planar case. Perhaps a method for computing loop hierarchies which is not based on the widths of the network branches could provide an answer. We hope that our approach of using algebraic topology language to deal with nodes and loops of networks will prove useful in developing such a method and complement other approaches.

Acknowledgments

References

[1] R. Albert and A. L. Barabasi. Statistical mechanics of complex networks. *Rev. Mod. Phys.*, 74:47–97, 2002.

[2] S Allesina, D Alonso, and M Pascual. A general model for food web structure. *Science*, 320:658–661, 2008.

[3] U. Alon. *An Introduction to Systems Biology: Design Principles of Biological Circuits.* Chapman and Hall/CRC, Boca Raton, FL, 2007.

[4] Uri Alon. Network motifs: theory and experimental approaches. *Nature Reviews Genetics*, 8(6):450–461, JUN 2007.

[5] Jayanth R. Banavar, Melanie E. Moses, James H. Brown, John Damuth, Andrea Rinaldo, Richard M. Sibly, and Amos Maritan. A general basis for quarter-power scaling in animals. *Proceedings of the National Academy of Sciences*, 107(36):15816–15820, 2010.

[6] A.-L. Barabasi. Network biology: understanding the cell's functional organization. *Nature Reviews Genetics*, 5:101–113, 2004.

[7] A.-L. Barabasi and R. Albert. Emergence of scaling in random networks. *Science*, 286:509–512, 1999.

[8] Marc Barthelemy. Spatial networks. *Physics Reports – Review Section of Physics Letters*, 499(1-3):1–101, FEB 2011.

[9] Benjamin Blonder, Cyrille Violle, Lisa Patrick Bentley, and Brian J. Enquist. Venation networks and the origin of the leaf economics spectrum. *Ecology Letters*, 14(2):91–100, FEB 2011.

[10] Bela Bollobas. *Modern Graph Theory.* Springer, 1998.

[11] Tim J. Brodribb, Taylor S. Feild, and Lawren Sack. Viewing leaf structure and evolution from a hydraulic perspective. *Functional Plant Biology*, 37(6):488–498, 2010.

[12] T.J. Brodribb, T.S. Feild, and G.J. Jordan. Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physol*, 144:1890–1898, 2007.

[13] J.H. Brown, J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. Toward a metabolic theory of ecology. *Ecology*, 77:1771–1789, 2004.

[14] Gary Chartrand. *Introductory Graph Theory*. Dover, 1985.

[15] Nicholas A. Christakis and James H. Fowler. The spread of obesity in a large social network over 32 years. *New England J. Med.*, 357(4):370–379, JUL 26 2007.

[16] H. Cochard, A. Nardini, and L.. Coll. Hydraulic architecture of leaf blades: where is the main resistance? *Plant Cell Environ.*, 27:1257–1267, 2004.

[17] Francis Corson. Fluctuations and Redundancy in Optimal Transport Networks. *Phys. Rev. Lett.*, 104(4):048703, JAN 29 2010.

[18] P. S. Dodds, R. Muhamad, and D. J. Watts. An experimental study of search in global social networks. *Science*, 301:827–829, 2003.

[19] P. S. Dodds and D. H. Rothman. Geometry of river networks III: Characterization of component connectivity. *Phys. Rev. E*, 63(1):016117, 2001.

[20] Peter S. Dodds and Daniel H. Rothman. Scaling, universality, and geomorphology. *Annu. Rev. Earth Planet. Sci.*, 28:571–610, 2000.

[21] PS Dodds, DH Rothman, and JS Weitz. Re-examination of the "3/4-law" of metabolism. *J. Theor. Biol.*, 209(1):9–27, MAR 7 2001.

[22] Natalie C. Duarte, Scott A. Becker, Neema Jamshidi, Ines Thiele, Monica L. Mo, Thuy D. Vo, Rohith Srivas, and Bernhard O. Palsson. Global reconstruction of the human metabolic network based on genomic and bibliomic data. *Proc. Natl. Acad. Sci. USA*, 104(6):1777–1782, FEB 6 2007.

[23] B.J. Enquist, J.H. Brown, and G.B. West. Allometric scaling of plant energetics and population density. *Nature*, 395:163–5, 1998.

[24] Cesar O. Flores, Justin R. Meyer, Sergi Valverde, Lauren Farr, and Joshua S. Weitz. Statistical structure of host-phage interactions. *Proc. Natl. Acad. Sci. USA*, 108(28):E288–E297, JUL 12 2011.

[25] M. T. Gastner and M. E. J. Newman. Optimal design of spatial distribution networks. *Physical Review E*, 74:016117, 2006.

[26] M Girvan and MEJ Newman. Community structure in social and biological networks. *Proc. Natl. Acad. Sci. USA*, 99(12):7821–7826, JUN 11 2002.

[27] R. Guimerà and L. A. N. Amaral. Functional cartography of complex metabolic networks. *Nature*, 433:895–900, 2005.

[28] R E Horton. Erosional development of streams and their drainage basins, hydrophysical approach to quantitative morphology. *Geological Society of America Bulletin*, 56(3):275–370, 1945.

[29] GS Kassab. Scaling laws of vascular trees: of form and function. *American Journal of Physiology - Heart and Circulatory Physiology*, 290(2):H894–H903, FEB 2006.

[30] Eleni Katifori, Gergely J. Szollosi, and Marcelo O. Magnasco. Damage and Fluctuations Induce Loops in Optimal Transport Networks. *Phys. Rev. Lett.*, 104(4):048704, JAN 29 2010.

[31] Tom Kolokotrones, Van Savage, Eric J. Deeds, and Walter Fontana. Curvature in metabolic scaling. *Nature*, 464(7289):753–756, APR 1 2010.

[32] Michael LaBarbera. Principles of design of fluid transport systems in zoology. *Science*, 249:992–1000, 1990.

[33] Kevin D. Lafferty, Andrew P. Dobson, and Armand M. Kuris. Parasites dominate food web links. *Proc. Natl. Acad. Sci. USA*, 103(30):11211–11216, JUL 25 2006.

[34] Tanya Latty, Kai Ramsch, Kentaro Ito, Toshiyuki Nakagaki, David J. T. Sumpter, Martin Middendorf, and Madeleine Beekman. Structure and formation of ant transportation networks. *Journal of the Royal Society Interface*, 8(62):1298–1306, SEP 7 2011.

[35] A. P. Masucci, D. Smith, A. Crooks, and M. Batty. Random planar graphs and the London street network. *Eur. Phys. J. B*, 71(2):259–271, SEP 2009.

[36] LA Meyers, B Pourbohloul, MEJ Newman, DM Skowronski, and RC Brunham. Network theory and SARS: predicting outbreak diversity. *J. Theor. Biol.*, 232(1):71–81, JAN 7 2005.

[37] A Nardini, MT Tyree, and S Salleo. Xylem cavitation in the leaf of Prunus laurocerasus and its impact on leaf hydraulics. *Plant Physiology*, 125(4):1700–1709, APR 2001.

[38] M. E. J. Newman. The spread of epidemic disease on networks. *Phys. Rev. E*, 66:016128, 2002.

[39] M. E. J. Newman. The structure and function of complex networks. *SIAM Review*, 45:167–256, 2003.

[40] MEJ Newman. Modularity and community structure in networks. *Proc. Natl. Acad. Sci. USA*, 103(23):8577–8582, JUN 6 2006.

[41] M. Pascual and J. Dunne, editors. *Ecological Networks: From Structure to Dynamics in Food Webs.* Oxford University Press, Oxford, UK, 2006.

[42] S. Peckham. New results for self-similar trees with applications to river networks. *Water Resour. Res.*, 31:1023–1029, 1995.

[43] J D Pelletier and D L Turcotte. Shapes of river networks and leaves: Are they statistically similar? *Phil. Trans. Biol. Sci.*, 355:307–311, 2000.

[44] C.A. Price and B.J. Enquist. Scaling of mass and morphology in Dicotyledonous leaves: an extension of the WBE model. *Ecology*, 88:1132–1141, 2007.

[45] Charles A. Price, Olga Symonova, Yuriy Mileyko, Troy Hilley, and Joshua S. Weitz. Leaf Extraction and Analysis Framework Graphical User Interface: Segmenting and Analyzing the Structure of Leaf Veins and Areoles. *Plant Physiology*, 155(1):236–245, 2011.

[46] N. Rashevsky. General mathematical principles in biology. In N. Raschevsky, editor, *Physicomathematical Aspects of Biology*, Proceedings of the International School of Physics "Enrico Fermi"; course 16, pages 493–524, New York, 1962. Academic Press.

[47] I. Rodriguez-Iturbe and A. Rinaldo. *Fractal River Networks: Chance and Self-Organization.* Cambridge University Press, New York, 1997.

[48] L Sack and NM Holbrook. Leaf hydraulics. *Ann. Rev. Plant. Biol.*, 57:361–381, 2006.

[49] Lawren Sack, Elisabeth M. Dietrich, Christopher M. Streeter, David Sanchez-Gomez, and N. Michele Holbrook. Leaf palmate venation and vascular redundancy confer tolerance of hydraulic disruption. *Proc. Natl. Acad. Sci. USA*, 105(5):1567–1572, FEB 5 2008.

[50] Van M. Savage, Eric J. Deeds, and Walter Fontana. Sizing Up Allometric Scaling Theory. *PLoS Comp. Biol.*, 4(9), SEP 2008.

[51] A N Strahler. Quantitative analysis of watershed geomorphology. *EOS, Transactions AGU*, 38:913–920, 1957.

[52] S.H. Strogatz. Exploring complex networks. *Nature*, 410:268–276, 2001.

[53] D. G. Tarboton, R. L. Bras, and I. Rodriguez-Iturbe. On the extraction of channel networks from digital elevation data. *Hydrological Processes*, 5:81–100, 1991.

[54] E Tokunaga. Consideration on the composition of drainage networks and their evolution. *Geogr. Rep. Tokyo Metro. Univ.*, 13:1–27, 1978.

[55] D. L. Turcotte, J. D. Pelletier, and W. I. Newman. Networks with side branching in biology. *J. Theor. Biol.*, 193:577–92, 1998.

[56] Y. Waisel, A. Eshel, and U. Kafkafi, editors. *Plant Roots: The Hidden Half.* CRC Press, 3 edition, 2002.

[57] D J Watts and S H Strogatz. Collective dynamics of 'small-world' networks. *Nature*, 393:440–442, 1998.

[58] G.B. West, J.H. Brown, and B.J. Enquist. A general model for the origin of allometric scaling laws in biology. *Science*, 276:122–126, 1997.

[59] K. Zhang and T. J. Sejnowski. A universal scaling law between gray matter and white matter of cerebral cortex. *Proceedings of the National Academy of Sciences*, 97:5621–5626, May 2000.